

Eichner, Thomas; Pethig, Rüdiger

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Thomas Eichner · Rüdiger Pethig

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Universität Siegen
Fakultät III
Wirtschaftswissenschaften, Wirtschaftsinformatik und Wirtschaftsrecht
Fachgebiet Volkswirtschaftslehre
Hölderlinstraße 3
D-57068 Siegen
Germany

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Economic Approaches to Ecosystem Analysis

Thomas Eichner and Rüdiger Pethig

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1 Reasons for and the potential of using economic methodology in ecosystem analysis

Ecological systems (*ecosystems*, for short) are complex systems of interacting species, plants and animals, where each of the species consists of individual organisms that *interact* with organisms of the same or other species in various ways: they compete for scarce resources and they are involved in predator-prey or mutualistic relationships. The challenge to understand the performance and changes of ecosystems over time was taken up long time ago by ecologists.¹

In the ecological literature² a vast number of models address ecosystem dynamics, taking populations as the relevant endogenous variables and investigating how populations develop and interact over time. For brevity, we call them *ecological population models*. Many of them focus on the simplest case of a single species as an aggregate entity developing over time. The prototype (heuristic) model for one large homogenous population in a constant environment is the *logistic growth curve* based on the so-called Verhulst-Pearl equation. Pierre Francois Verhulst (1838) introduced the logistic equation and Raymond Pearl (1930) applied it to population growth in the US; this equation turned out to become an important analytical tool in ecosystem analysis.

Modeling dynamic multi-species intra-ecosystem interdependence and interaction increases the level of complexity significantly. It is convenient to characterize multi-species models according to which type of interaction they focus on: (a) competition for resources, (b) predator-prey relations and (c) mutualism. The analysis of both (a) and (b) originated in the pioneering contributions of Lotka (1925) and Volterra (1926). Larkin (1963,1966) and Gause (1964) elaborated on the Lotka-Volterra approach and extended it in various important ways.

- *Competition* among interacting species may take the form of competition for food, water or habitat. It is modeled through introducing competition coefficient and limited resource capacities. For more details, see Tilman (1980, 1982, 1985), Pacala and Tilman (1994) and Roughgarden (1998).

¹ Ecosystems analysis is a core area of research for biologists, but other natural scientists like physicists and chemists are also involved. For convenience, we call ecologists all natural scientists whose focus are ecosystems.

² For surveys of mathematical modeling of ecosystems see e.g. Murray (1993) and Brown and Rothery (1993).

- Two-species models are the simplest way to study dynamic *predator-prey relations*. With more than two species the analysis becomes very involved (or even intractable), in particular, when the food chain is not unidirectional. See, e.g. Bulmer (1976), Brauer and Sontack (1979), May (1981) or Ragozin (1982).
- *Mutualism* denotes the phenomenon of two or more species promoting each other's growth. For example, one species generates outputs or resources that foster another species' population growth. Mutualistic systems are studied e.g. by Goh (1979) and Travis and Post (1979).

Over the last decades evidence accumulated about serious detrimental effects or 'environmental damage' many economic activities inflict on ecosystems and about the feedback of these ecological disruptions on the economy. In fact, it is this mutual dependence between the ecosystem and the economic system that spurred the interest for better understanding how exactly ecosystems work, what the interface between both systems is like and how changes in one system impact on the other.

To date, significant progress has been made towards answering these questions. A growing ecological literature emerged focusing on the impact on ecosystems of economic activities including harvesting, pollution, irrigation, deforestation or other changes in land use configurations (e.g. Shukla and Dubey (1997), Namba, Umemoto and Minami (1999) and Dubey and Hussain (2000)). However, ecologists use to model economic activities in a rudimentary way only. They introduce parameters whose (exogenous) changes cause populations to adjust. On the other hand, economists also took into account that some economic activities have detrimental impacts on ecosystems and responded by extending their models (of the economy) to capture pollution and 'environmental damage'. However, in its core the by now well established branch of environmental economics is still a theory of environmental externalities in which the environment-economy interactions play a minor, if not even a marginal role only. Essentially the ecosystem is treated as a black box hidden behind damage functions whereas intra-economy interactions use to be modeled in a much more complex and elaborate way.

More recently, some progress has been made in opening up that black box by integrating intra-economy and intra-ecosystem interactions with special emphasis on the interface of both systems. The economy is represented by a set of differential or difference equations and the ecosystem is represented by ecological population models. This framework allows to characterize Pareto efficient (economic!) allocations and market allocations accounting for economic and ecological constraints that have been included in the model. Clark and Munro (1975), Ströbele and Wacker (1995) and Brack and Xepapadeas (1998, 2000) are major contributions to this approach. Clark and Munro (1975) address the issue of (efficient) harvesting in an ecosystem consisting of a single species whose population dynamics satisfy the Verhulst-Pearl equation. Their model is extended by Ströbele and Wacker (1995) to a two-species ecosystem and by Wacker (1999) to an ecosystem with mutualistic interactions. Brock and Xepapadeas (1998, 2000) investigate optimal ecosystem management in a competitive economy.

This dynamic approach to ecosystem-economy interaction is valuable, because it is balanced in its treatment of intersystem-interactions combined with intrasystem-interactions in both systems. It is also ambitious regarding the mathematical tools applied. Unfortunately, however, the insights to be gained are limited because the analysis becomes very involved or even intractable as soon as either system is modeled in a realistic, that is complex way. Brock and Xepapadeas (1998, 2000) provide an illustration of this point: The decision problems of the social planner and the market participants are so complex that hardly any specific unambiguous conclusion can be reached. Hence this approach will promise only little mileage on the conceptual level. But on the other hand, it lends itself well to numerical analysis, and with mod-

ern computing tools it is in this area of applied research where its strengths have been and will continue to be demonstrated. Needless to say that analytical – as opposed to numerical - intractability seems to be the fate of all pretentious complex dynamic ecosystem-economy models. In view of this dilemma there is certainly some merit in ‘unbalanced’ approaches to ecosystem-economy interactions in either direction: the environmental economist’s tendency to reduce the ecosystem complexity may be appropriate *for some issues* and the ecologist’s tendency to reduce the complexity of the economy *for others*.

Having made the case for not discarding of conventional 'unbalanced' approaches we hasten to add that large-scale integration of both systems remains indispensable for a full understanding of the complex interdependencies in and between these systems. How good our understanding is depends, in turn, on the methodology of modeling. In our view, combining an economic model with the ecological population is not yet completely satisfactory for the following reasons:

Ecological population models represent a macro approach where the relevant variables typically are aggregate interdependent populations. The focus is on populations changing over time and responding to shocks (parameter changes). For example, a predator species population is assumed to increase, *ceteris paribus*, following a shock-induced increase in a prey population. There is nothing wrong with the plausibility or even empirical relevance of such hypotheses. The point rather is a methodological one: Taking populations as the basic endogenous variables implies to *disregard* – and hence fail to explain - the fact that intra-ecosystem transactions of biomass take place: biomass flows from individual organisms of prey species to individual organisms of predator species and where most organisms are predators as well as preys. From a species perspective, preying is vital for surviving, and surviving presupposes, in turn, that a predator’s prey species survive(s).

Pursuing the end of developing a fully integrated analysis of both systems without resorting to ecological population models begs the question as to which methodology of ecosystem analysis should be chosen as an alternative. It is clear that we need to go for a compatible – or maybe even for a joint - methodology since otherwise the interface of both systems would not be well defined. In computer science, hardware components cannot communicate without standardized interfaces. For similar reasons, we need an appropriate method of integrated ecosystem-economy analysis with the capacity to study repercussions in one of the systems caused by shocks in the other.

Owing to their background in economics, some environmental economists maintain that, for the purpose of integration, ecosystem analysis should be further (or re-) developed using economic methods. This is a contentious methodological route which some researchers, non-economists in particular, might be reluctant to follow. Nevertheless, from a pragmatic perspective, there are good reasons to embrace this proposition simply because the analysis of the economy is based on a powerful and well-established methodology. If major elements of this methodology were applied to ecosystem analysis one could hope for interesting new insights in the interactions between both systems. The present paper aims at discussing major pieces of economic methodology suggested for ecosystem analysis in the literature and at examining their potential of reshaping ecosystem analysis to make it fit for a balanced two-pillar integrated analysis of both systems.

With respect to their micro structure ecosystems are strikingly similar to economies: Characteristic for both systems are the production of outputs by means of primary inputs and intermediate products and a network of transactions between agents. It is tempting, therefore, to explore how far this purely formal analogy can be carried, or more specifically, how fruitful it is to study intra-ecosystem interaction using economic methodology. A major point of dissent,

if not the central one, for applying economic theoretical concepts to ecosystem analysis is probably the economists' preoccupation with teleology and rationality. In economics, competitive markets or social planners, for that matter, are considered to maximize natural product, consumers maximize utility and producers maximize profits under appropriate constraints. There are good reasons to doubt whether maximizing or optimizing of some sort is part of nature's blueprint. This contentious issue will be further discussed below. And yet, there is already a small literature that studies ecosystems with economic methodology including production, prices and optimizing behavior. Two major lines of research can be distinguished.

The first line takes up Koopmans' (1951) linear production model of an economy and applies it to ecosystems (Amir (1989, 1994) and Klauer (2000)). These authors focus on biomass transfers in predator-prey relationships and on the species' use of ecosystem endowments of nutrients like water, minerals, solar energy etc. and establish a short-run ecosystem equilibrium suggesting that the ecosystem *as a whole* thrives for 'production efficiency'. Short-run equilibria are then linked by suitable stock-flow conditions to result in a dynamic model of changing populations. This approach is more elaborate than the standard ecological population model in that the process of transforming inputs into outputs is explicitly taken into consideration. On the other hand, it shares with the ecological approach the feature – or perhaps the shortcoming – that its principal focus is also on aggregate entities (populations). Quite obviously, each species inhabiting a given ecosystem consists of a number of individual organisms and interactions take place between members of the same species as well as between individuals of different species. Populations do not interact with populations neither mechanically as in the ecological model, nor guided by some central maximizing 'ecological' planner. It is the activities (or behavior) of all individual organisms that drive the ecosystem dynamics. In other words, both the ecological population model and the linear production approach lack a microfoundation – as economists would call it – or the individual base (Judson (1994)): they ignore individual behavior and (hence) do not explain community structure as resulting from individual activities.

Responding to this criticism, the second line of research aims at microfounding the ecosystem analysis using the assumption familiar to economists that (representative) individual organisms of each species maximize – or behave as if they maximize – some objective function under pertinent constraints. There is little consent about what the appropriate maximand is. Among the maximands suggested in the literature are energy (Lotka 1922, Hannon 1973, 1976, 1979, Tschirhart (2000)), biomass (Odum 1969, Reichle et al. 1975, Whittaker 1975), power (Odum and Pinkerton 1955, Odum 1971), energy (Jorgenson 1982, 1986) and ascendancy (Ulanowicz 1986). A common feature of microfounded ecosystem analysis with (as if) maximizing agents is that non-linear technologies are employed and that short-run price-supported ecosystem equilibria are established which are then connected via stock-flow relations to form dynamic time-paths of moving short-run equilibria.

After this brief introduction into the motivation for and the potential of using economic methodology in ecosystem modeling we now proceed to describe and compare in more detail the two main concepts introduced above. Section 2 elaborates on the linear production model and in section 3 the issue of microfoundation and substitutional biomass production technology is discussed. Section 4 concludes.

2. The linear production approach to ecosystems

In economics, linear production models and/or their application in input-output analysis have been studied by von Neumann (1945), Koopmans (1951), Leontief (1951) and Malinvaud (1953). The linear production approach was applied to ecosystems by Amir (1989,1994) and Klauer (2000). For a given period, an *economic* linear production model has the following structure:

$$z_i = \sum_j a_{ij} \cdot z_j + q_i \quad i = 1, \dots, m \quad (1)$$

$$\sum_j b_{ij} \cdot z_j \leq r_i \quad i = 1, \dots, n \quad (2)$$

z_i = gross output of sector i (gross output i)

q_i = net output of sector i (net output i)

r_i = total exogenous endowment of primary factor i

a_{ij} = constant production coefficient, determining the amount of output i needed as an intermediate product by sector j per unit of output j

b_{ij} = constant input of primary factor i needed by sector j per unit of output j

All variables and parameters listed above are non-negative. For convenience, we define

$$q := (q_1, \dots, q_n), \quad p := (p_1, \dots, p_n), \quad \text{the price simplex } P := \left\{ p \geq 0 \mid \sum_{j=1}^n p_j = 1 \right\} \text{ and}$$

the production possibility set $Q := \{q \mid q \text{ satisfies (1), (2) and } q \geq 0\}$

Koopmans was interested in identifying and characterizing efficient net output vectors in the set Q of feasible net outputs. By definition, an output $q \in Q$ is *efficient*, if there is no $q' \in Q$ such that $q'_i \geq q_i$ for all i with the strict inequality holding for at least one net output i . The appeal of this 'production efficiency' property (also called Koopmans efficiency) is that no inputs or outputs are wasted. Koopmans' (1951) important contribution was to show that $\tilde{q} \in Q$ is *efficient if and only if there is* $\tilde{p} \in P$ *such that*

$$\sum_{j=1}^n \tilde{p}_j \cdot \tilde{q}_j \geq \sum_{j=1}^n \tilde{p}_j \cdot q_j \quad \text{for all } q \in Q. \quad (3)$$

The equivalence property of this theorem is remarkable: for a given suitable p we find an efficient $\tilde{q} \in Q$ through (3), and conversely, for any given efficient $\tilde{q} \in Q$ we find a price vector, namely $\tilde{p} \in P$, such that (3) holds. The latter observation means that *dual* to every efficient production are (shadow) prices that reflect the 'true' scarcity or abundance of all output components of \tilde{q} .

Koopmans approach is translated into a model of an ecosystem as follows. The sectors are species and z_i is the gross biomass of species i . $a_{ij} \cdot z_j$ is the amount of own biomass species i passes to predator species j when j 's gross biomass is z_j . Hence (1) captures all biomass transactions from prey to predator species. r_i is the ecosystem's endowment of nutrient i , e.g. solar energy, water, minerals etc., and $b_{ij} \cdot z_j$ is the demand of nutrient i by species j when j 's gross biomass is z_j .

Given this reinterpretation of terms, q_i clearly is the net biomass of species i acquired in the period under consideration after having ‘served’ all its predators. In full analogy to Koopmans, Klauer (2000) proceeds by assuming that the ecosystem as a whole strives for maximizing the value of total net biomass, $\sum_j p_j \cdot q_j$, for some suitable price vector p subject to the constraints (1) and (2). The solution to this optimization calculus, say $q^* \in Q$, represents the net biomass all species acquired in the period under consideration. Invoking Koopmans’ (1951) theorem referred to above we know that q^* is efficient. In other words, the thrust of this ecosystem model is the claim, that ecosystems use their nutrient endowment and their biomass transfers to predators in an efficient, i.e. non-wasteful way.

It is not quite clear, however, what role is assigned to and how to interpret the maximizing procedure in Klauer’s model. Is the idea, as we conjectured above, to start out with a price vector, say $\tilde{p} \in P$, and arrive at $\tilde{q} \in Q$ satisfying (3)? The trouble with this interpretation is, though, that it remains unexplained how the ecosystem picks the prices \tilde{p} in the first place. Alternatively, we can reverse the role of prices and quantities by starting with the proposition (or rather the claim) that the ecosystem generates an efficient vector of net biomass, $\tilde{q} \in Q$. Then we calculate the associated ‘efficient prices’ informing us about scarcity. But unfortunately, this procedure leaves unexplained how the efficient net biomass $\tilde{q} \in Q$ was attained.

The linear production model discussed so far is static and designed to describe a one-period ecosystem equilibrium. An extension towards ecosystem dynamics has been suggested by Amir (1995) who modified equation (1) to read

$$q_i = \sum_j a_{ij} \cdot z_j - z_i - \frac{ds_i}{dt} \quad i = 1, \dots, m, \quad (4)$$

where s_i is species i ’s stock of total biomass accumulated in the past.

While the standard ecological model focusses on the interaction of species populations in a rather mechanical way, the linear production model has two important additional features: it considers explicitly production processes within the ecosystem, i.e. the processes of transforming inputs (nutrients and prey biomass as intermediary products) into outputs (the species’ gross biomass) and it designs the ecosystem as an efficiency-oriented entity.

In our view, the explicit modeling of intra-ecosystem production and transactions is an indispensable part of realistic ecosystem analysis. However, the linearity of the production technology does not appear to be an acceptable assumption. To see that consider a species i and suppose, for ease of exposition, that $a_{ji} > 0$ for all $j = 1, \dots, m$ and $b_{ki} > 0$ for all $k = 1, \dots, n$. Let $r_{ki} \geq 0$ be the amount of nutrient k available to species i and let x_{ji} be the amount of biomass of (prey) species j available to species i . Then species i ’s gross biomass ‘produced’

with the help of the inputs $r_{1i}, \dots, r_{ni}, x_{1i}, \dots, x_{mi}$ is $x_i = \min \left[\frac{r_{1i}}{b_{1i}}, \dots, \frac{r_{ni}}{b_{ni}}, \frac{x_{1i}}{a_{1i}}, \dots, \frac{x_{mi}}{a_{mi}} \right]$. Given

this Leontief technology, an efficient production clearly requires to use all inputs in strict proportion, i.e. $r_{1i} = \frac{b_{1i}}{b_{2i}} \cdot r_{2i} = \dots = \frac{b_{1i}}{b_{ni}} \cdot r_{ni} = \frac{b_{1i}}{a_{1i}} \cdot x_{1i} = \dots = \frac{b_{1i}}{b_{2i}} \cdot x_{mi}$.

In contrast to this specification of production, (casual) empirical observation suggests that most species are capable to substitute nutrients and/ or prey species, in a certain range at least, without serious harm to their ‘well being’. For detailed empirical evidence see, e.g., Meneg (1972) or Bantell (1982). Tschirhart (2001) is therefore correct in pointing out that organisms substituting among prey as a reaction to changing environments are a key feature of ecosys-

tems. It is desirable, therefore, to employ substitutional production technologies for modeling ecosystems.

Before we address this issue in the next section a final remark is in order on how the linear production approach solves the resource allocation problem using the maximizing procedure (3). Efficiency is reached as if the ecosystem as a whole is guided by Adam Smith's invisible hand without any explanation as to how this result is brought about by the ecosystem's inhabitants. To be sure, the efficiency result has considerable appeal not only to economists who are vastly preoccupied with allocative efficiency in their modeling. The idea that nature economizes on its use of scarce natural resources through evolutionary selection has been put forward since long in many contexts. However, the problem we have with the maximizing procedure (3) is that it is related to aggregate variables, the gross biomass of species. This maximization 'from the top' leaves open the questions why and how the individual organisms take the path towards efficiency. We now turn to investigate whether further insights into the forces driving ecosystems can be gained through a microfoundation of ecosystem analysis.

3 Microfounded ecosystem analysis with non-linear production technology

Since the demand for microfoundation is a crucial methodological issue, let us briefly point out, by way of digression, its role in economics. To begin with, an economy and an ecosystem are similar in that both consist of many agents. (In fact economies are simpler because *homo sapiens* is the only species). In both systems all agents exhibit an observable behavior - whatever their motives, incentives or genetic driving forces are. In economics, the behavioral hypotheses of firms maximizing profits and consumers maximizing utility under appropriate constraints are widely accepted in theoretical analysis, even though some economists and many non-economists do challenge these assumptions on both empirical and conceptual grounds. Leaving this ongoing dispute aside, we like to emphasize that it is the assumption of maximizing behavior that provides the microfoundations of aggregate demand and supply curves. Microfoundation of this type has become a widely accepted methodological standard in economics so much so that ad hoc macro-analyses are not readily accepted any more by many economists.³

"But in an ecosystem, do nonhuman organisms maximize? Most people do not credit a weasel with thoughtful preference revelation when it raids the chicken coop instead of ferreting out a mouse or two. '... men consciously optimize, animals do not - they survive by adopting successful strategies 'as if' conscious optimization takes place' (Hirshleifer, 1977, p. 4). This "as if" assumption is sufficient to capture much of the behavior of nonhuman organisms and thereby establish a fruitful model." [Crocker and Tschirhart, 1992, p. 555]

We believe that this quotation from Crocker and Tschirhart provides a convincing justification for treating individual organisms as maximizers while we are aware of others who consider this methodological approach inappropriate. Peters (1991) welcomes it as a fruitful source of testable hypotheses. Tschirhart (2001, p. 4) finds the optimizing approach useful because it "... presents mechanisms through which: 1) more efficient resource use by an organism leads to greater success, and 2) interactions among individual organisms lead to observed dynamics in ... [species] communities."

³ In this context it is interesting to observe that its lacking microfoundation was considered a serious flaw of the Keynesian macroeconomic theory by many economists. Modern macroeconomics tends to be microfounded or even converges towards microeconomics.

3.1 Hannon's concept of energy maximizing organisms

According to Hannon (1976, p. 535) the currency in natural systems is energy. Herendeen (1991) observes that energy has been the most frequently chosen maximand. Species obtain energy from sunlight or from feeding on other species and they lose energy to other species when they are preyed upon. In addition, they need energy for 'maintenance', i.e. for respiration, metabolism etc. Another important currency in ecosystems is biomass measured, e.g., in kilograms. Hannon (1976) and Tschirhart (2000) assume that the energy embodied or stored in each unit of biomass is (roughly) constant and species-specific. Denote by e_i the energy embodied per unit of biomass from an individual organism of species i . Clearly, with the 'exchange rate' e_i constant both currencies are equivalent dimensions for ecosystem analysis.

We now envisage an ecosystem with m species, among them plants and animals, and consider for each of these species $i = 1, \dots, m$ a representative individual organism called *organism i* , for short. The only nutrient, which is explicitly accounted for is sunlight. It is analytically convenient to refer to the sun as species 0 and to think about plants as preying on that species. Hannon (1976) and Tschirhart (2000) modeled a unilateral non-circular food chain. We will use a more general formulation and define for this purpose:⁴

$$M := \{0, 1, 2, \dots, m\}, \quad A^i := \{j \in M \mid j \text{ is a predator species for } i\},$$

$$B^i := \{j \in M \mid j \text{ is a prey species for } i\}$$

Observe that $A^0 = \emptyset$ and that the existence of plants is secured by $0 \in B^i$ for some $i > 0$. The demand of organism i for biomass of organism j is denoted x_{ij} and the supply of organism i 's own biomass to organism j is denoted y_{ij} . We set

$$x_{ij} \begin{cases} \geq 0 & \text{for } j \in B^i, \\ \equiv 0 & \text{otherwise,} \end{cases} \quad \text{and} \quad y_{ij} \begin{cases} \geq 0 & \text{for } j \in A^i, \\ \equiv 0 & \text{otherwise,} \end{cases}$$

and write for compactness $x^i := (x_{i1}, \dots, x_{im})$ and $y^i := (y_{i1}, \dots, y_{im})$.

The central building block of Hannon's (1976) model is the net energy of organism i , defined (in Tschirhart's (2000) specification) as

$$v_i = \sum_{j \in B^i} (e_j - e_{ij}) \cdot x_{ij} - \sum_{k \in A^i} e_i \cdot y_{ik} - F^i(x_i) - \beta_i \quad (5)$$

In (5) e_{ij} is the energy to be spent by i to locate and capture a unit of biomass of j ; the 'energy price' e_{ij} is constant from i 's perspective but endogenous in the system as a whole. β_i is a constant reflecting basal metabolism, independent of energy intake. The function F^i in (5) reflects that part of metabolism and respiration which depends on the energy intake.

At first glance, (5) bears little resemblance with the linear production approach. To clarify the relationship it is helpful to rewrite (5) by separating the dimensions of energy and biomass. For that purpose we define

⁴ The special case of an unilateral food chain is defined by the constraints: ($j \in A^i \Leftrightarrow j > i$ for all $i \in M$) and ($j \in B^i \Leftrightarrow j > i$ for all $i = 1, \dots, m$). It is interesting and convenient for specific empirical applications but it is unnecessarily restrictive for the purpose of conceptual analysis.

$$q_i := \frac{v_i}{e_i}, \quad H^i(x_i) := \frac{F^i(x_i)}{e_i}, \quad \gamma_i := \frac{\beta_i}{e_i}, \quad c_{ij} := \frac{e_j}{e_i} \quad \text{and} \quad p_{ij} := \frac{e_{ij}}{e_i}. \quad (6)$$

Inserting (6) in (5) yields

$$e_i \cdot q_i = e_i \cdot \left[Z^i(x^i, p^i) - \sum_{k \in A^i} y_{ik} \right] \quad (7)$$

with

$$Z^i(x^i, p^i) := \sum_{j \in B^i} (c_{ij} - p_{ij}) \cdot x_{ij} - H^i(x^i) - \gamma \quad (8)$$

and $p^i := (p_{i1}, \dots, p_{in})$. If we refer to the generation of own biomass as (gross) output of i , then Z^i is clearly the production function of gross output i . The vector p^i affects factor productivity such that productivity shrinks when some component p_{ij} is increased. Recall that p_{ij} (or rather e_{ij}) is exogenous to the individual organism i but will be determined endogenously in short-run ecosystem equilibrium. We refer to p^i as unit *predation costs* of organism i (in terms of own biomass per unit of preyed biomass). It turns out, then, that (5) is the value of net biomass i , defined as the difference between the value of gross biomass i , $e_i \cdot Z^i(\cdot)$, and the value of own biomass to be supplied to prey species, $e_i \cdot \sum_{k \in A^i} y_{ik}$. Observe also that our

transformation of (5) into (7) reveals the possibility of carrying out the entire analysis on the basis of biomass rather than energy.

Following the basic rationale of the linear production approach, Hannon (1976) and Tschirhart (2000) proceed to take the energy value of net biomass as the organism's maximand. The decisive difference to section 2 is that maximization is now assumed to take place at the micro level, and is hence a behavioral or an 'as if' behavioral assumption. The intakes x^i are clearly variables under control of organism i , but the outflows y^i are not. Therefore, the maximization problem for the individual organisms is not well defined. This difficulty is overcome by introducing the additional assumption that organisms "...are subject to predation risk and the biomass they supply depends on the biomass they demand" (Tschirhart 2000). Formally, for all i we have

$$y_{ik} = Y^{ik}_+(x^i) \quad k = 1, \dots, n \quad (9)$$

which turns (7) into

$$e_i \cdot Q^i(x^i, p^i) := e_i \cdot [Z^i(x^i, p^i) - \sum_k Y^{ik}(x^i)]. \quad (10)$$

We assume that $Q^i(x^i, p^i)$ is strictly concave in x^i and attains, for any given p^i , a maximum at

$$X^i(p^i) := \arg \max_{x^i} e_i \cdot Q^i(x^i, p^i). \quad (11)$$

(11) establishes organism i 's demand for biomass as a function of unit predation costs p^i .

3.2 Short-run ecosystem equilibrium

In the short-run, all populations n_1, \dots, n_m are given. The basic equilibrium condition for a (short) period is that for each pair of species i and j the following equation holds:

$$n_i \cdot x_{ij} = n_j \cdot y_{ji} \quad i, j = 1, \dots, m, i \neq j \quad (12)$$

In view of (9) and (11) we rewrite (12) as

$$n_i \cdot X^i(p^i) = n_j \cdot Y^{ji} \left[X^j(p^j) \right] \quad i, j = 1, \dots, m, i \neq j. \quad (13)$$

A short-run equilibrium is defined by a vector of predation costs $p := (p^1, \dots, p^m)$ such that (13) is satisfied. (13) consists of $m \cdot (m-1)$ equations to determine the $m \cdot (m-1)$ variables p .⁵ Clearly, to demonstrate the existence of a short-run equilibrium in a rigorous way, it is necessary to construct an appropriate fixed point argument. Hannon (1976) did not address the issue of short-run equilibrium. Tschirhart (2000) defines the equilibrium via (12) and (13) and demonstrates the existence for numerical examples, but a general existence proof is still missing to our knowledge.

Assuming that existence is secured under sufficiently general assumptions, it is important to understand the nature of a short-run equilibrium. The principal advantage of the ecosystem equilibrium approach of Hannon and Tschirhart over the linear production model is its capacity to fully determine the allocation of all resources: the use of solar energy, the intermediate flows of prey biomass as well as all organism's net energies and predation costs. This gives the model great predictive power provided it can be calibrated with empirically relevant data. Admittedly, multiple equilibria may cause problems in this respect but economists have to cope with the same type of difficulties in modeling perfectly competitive economies.

Obviously, the driving force of bringing an equilibrium about is the appropriate adjustment of predation costs. At first glance, the predation cost p^i of organism i may be viewed as a negative externality affecting this organism's biomass production function. However, p^i is not an activity under control of any other agent, which one needs to require for referring to p^i as an externality. In the Hannon-Tschirhart model, predation costs rather play the role market of clearing prices in economic models. In other words, endogenous predation costs are the model's (only!) equilibrating mechanism. As a consequence, it is not clear how to assess the (in-)efficiency of the equilibrium allocation. For an economist, flexible predation costs 'designed' to guide the ecosystem into short-run equilibrium are a highly unfamiliar concept. In economic modeling, technologies may well be affected by externalities but we are not aware of economic analyses with technologies subject to variables whose values are chosen, like prices, exclusively to the end of reaching an equilibrium. We find it difficult to offer a convincing interpretation and justification for this procedure.

The second central feature of the model, which diverges squarely from economic modeling, is the assumption (9) according to which organism i 's supply of own biomass is completely determined by its own demand for prey biomass. When preying on other species organism i exposes itself to its enemies, and this predation risk is indeed a plausible reason to relate x^i and y^i . It is true that some kind of relation between purchases and expenditures also exists in economic modeling since a firm's purchases of inputs are related to its sales via profit maximiza-

⁵ The vector p is m^2 -dimensional but $p_{ii} \equiv 0$ for all $i = 1, \dots, m$.

tion and a consumer's sales of labor are related to his or her purchases of consumer goods via the budget constraint. But a deterministic link as in (9) appears to be a very restrictive assumption that is hard to accept. Assuming that an economic agent's supply of goods is determined by his or her demand for goods would appear to be an rather strange proposition.

3.3 Ecosystem dynamics

Given a short-run equilibrium, the decisive question is how to model the ecosystem's 'law of motion' in time. To be more specific, suppose $n_t := (n_{1t}, \dots, n_{mt})$ are the species' populations in some period t and

$$p_t := (p_t^1, \dots, p_t^m) = P(n_t) \quad (14)$$

are the equilibrium predation costs in period t . Then the associated net biomass of the representative organism of species i is

$$q_{it} := Q^i[X^i(P(n_t)), P(n_t)] := \hat{Q}^i(n_t). \quad (15)$$

Tschirhart's (2000) basic assumption is that (with discrete notation of time)

$$n_{i,t+1} - n_{it} \begin{cases} > \\ = 0 \\ < \end{cases} \Leftrightarrow \hat{Q}^i(n_t) \begin{cases} > \\ = 0 \\ < \end{cases} \quad (16)$$

He then points out that many different methods for adjusting populations could be introduced, and he suggests a specific procedure based on the Verhulst-Pearl logistic equation combined with the concept of species-specific carrying capacities that are endogenized via (16). Rather than discussing this elaborate approach in more detail we choose to illustrate here another simple and, as we believe, straightforward link between short-run equilibrium and intertemporal species dynamics: Let b_i be the average biomass of an organism of species i so that $n_{it} \cdot b_i$ is species i 's total biomass in period t . Moreover, interpret $\hat{Q}^i(n_t)/b_i$ as the (positive or negative) number of new organisms to which the representative organism of species i gave birth, on average, during period t (where all new organisms are assumed to be grown up immediately). The change in population is therefore $n_{i,t+1} - n_{it} = n_{it} \hat{Q}^i(n_t)/b_i$ implying that the growth rate of the population of species i is

$$\frac{n_{i,t+1} - n_{it}}{n_{it}} = \frac{\hat{Q}^i(n_t)}{b_i}. \quad (17)$$

As long as $\hat{Q}^i(n_t) \neq 0$, the population of species i grows or shrinks. Hence a *long-run ecosystem equilibrium or a steady state of the ecosystem* is attained, if and only if there is some period t such that $n_{i,t+\tau} = n_{it}$ for all $\tau > 0$ and for all $i = 1, \dots, m$. To calculate such a steady state one has to solve for n_t the m equations

$$\hat{Q}^i(n_t) = 0 \quad \text{for } i = 1, \dots, m. \quad (18)$$

Note, however, that (18) may fail to have a solution or that (18) may have multiple solutions. Moreover, even if a solution to (18) exists, it is an open and not at all trivial question whether the steady state will be reached from some given (non steady-state) initial situation.

3.4 An alternative approach to modeling plants

In the Hannon-Tschirhart model discussed above plants are defenceless prey of herbivores and feed on sunlight. Their access to sunlight is bounded from above by e_o but will be further reduced, in general by positive predation cost e_{io} (here: cost of access to sunlight or access cost, for short). This access cost is beyond the plants' control, but it is endogenously determined in the ecosystem. Plant i 's production of biomass is less productive, ceteris paribus, the less access it has to sunlight, i. e. the smaller is $(e_o - e_{io})$. While the thrust of this argument is appealing, the downside is that the model does not explain why and how changes in the cost of sunlight access are bought about.

Pethig and Tschirhart (2001) suggested to explicitly incorporate the determinants of changes in the cost of access to sunlight into the formal analysis. In their model, animal species are suppressed altogether, so that⁶ $Q^i(x_{io}, p_{io}) = Z^i(x_{io}, p_{io})$ for all plant organisms i . The central hypothesis is that

$$p_{io} = P^{io}(x_o, n) \quad i = 1, \dots, m \quad (19)$$

where $x_o := (x_{1o}, \dots, x_{mo})$ and $n := (n_1, \dots, n_m)$. The idea behind (19) is that the ecosystem is a natural system with limited space to which all plants have free access. As long as populations and plant biomass are small, access costs p_{io} are zero. However, with increasing biomass and populations, crowding or congestion sets which in turn diminishes all plants' exposure to sunlight. A simple but illustrative specification of (19) is given by

$$P^{io}(x_o, n) = \max \left[0, \sum_{j=1}^m x_{jo} n_j - \bar{a}_i \right] \quad (19')$$

where \bar{a}_i is a positive constant.

Let $p := (p_{1o}, \dots, p_{mo})$ be the prevailing access cost which all plants take as given. The plants' demand for sunlight is then given by $X^i(p_{io})$, essentially as in (9). A short-run ecosystem equilibrium is a pair (\hat{p}, \hat{x}_o) for given populations n , such that

$$\hat{p}_{io} = P^{io}(\hat{x}_o, n) \quad \text{and} \quad \hat{x}_{io} = X^i(\hat{p}_{io}) \quad \text{for all } i = 1, \dots, m \quad (20)$$

To model the dynamics of the plant ecosystem model, we proceed as in the last section. Let $\hat{p} = \hat{P}(n_t)$ be the vector of access costs associated to the short-run equilibrium in some given period t and define

$$\hat{Q}^i(n_t) := Q^i \{ X^i[\hat{P}(n_t)], \hat{P}(n_t) \} \quad i = 1, \dots, m \quad (21)$$

as in (15). With $\hat{Q}^i(n_t)$ from (21) the dynamics are the same as those described in the last part of section 3.3 following equation (15).

Comparing the treatment of plants in the Hannon-Tschirhart model and the Pethig-Tschirhart model shows that in the latter the sunlight access costs are determined by a process of conges-

⁶ Pethig and Tschirhart use energy as currency. We describe their model here in terms of biomass for the benefit of comparability with the approach of the preceding sections.

tion or crowding familiar from the economic allocation literature on free access resources. The phenomenon of crowding is an inevitable consequence of free access whether plant competition for access to sunlight is at issue or crowded highways and traffic jams. The established economic methods to analyze the latter appear to be appropriate for studying the former. The substantial benefit of modeling sunlight access costs by means of congestion is that these costs are now determined by an externality proper as economists use that concept. In contrast, in the Hannon-Tschirhart model the determinants of sunlight access costs - and predation costs more generally - are the unspecified, hidden forces that equilibrate all intermediate demands and supplies of biomass.

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